

Correlates of Vertebrate Extinction Risk in Canada

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Species status assessments are often hindered by a paucity of demographic, abundance, or distributional data. Although extinction-risk correlates have been identified, their wide applicability may be compromised by differences in the variables examined, modeling technique, and phylogenetic or distributional scale. Here, we apply a common analytical approach to examine 14 possible extinction-risk correlates for mammals, fishes, and birds throughout Canada. Among mammals, risk is positively and strongly correlated with road density and age at maturity for land animals and weakly with body size for sea dwellers. Delayed maturity is of primary importance to predicting risk status in fishes, with small body size of secondary importance in freshwater environments. For birds, road density is the dominant correlate of risk. Logistic regression in a multimodel framework offers an instructive means of identifying risk correlates and of applying them in a practicable, empirically defensible manner, thus enhancing support for species-independent risk criteria.

Keywords: life history, mammals, fishes, birds, human impact, COSEWIC

International concerns about global and regional reductions

In the abundance of plants and animals have hastened efforts to identify correlates of extinction risk in a wide variety of species (Purvis et al. 2000a, 2000b). Such correlates are particularly important in that they can enable the rapid assessment of poorly understood species groups on the basis of their similarities to more heavily studied taxonomic or geographic neighbors. Concomitant with this work is the question of whether extinction-risk correlates are likely to differ among species groups or whether the correlates are sufficiently similar that one might be justified in applying risk-assessment criteria and associated thresholds to assessments of species status that are independent of taxonomic affiliation (Mace et al. 2008).

The study of extinction-risk correlates has, to date, been focused primarily on vertebrates. Body size, for example, is positively associated with extinction risk in many groups—for instance, birds (Bennett and Owens 1997); terrestrial mammals (Cardillo et al. 2005); marine mammals (Dulvy et al. 2003); and marine fishes (Jennings et al. 1998), although both small- and large-bodied freshwater fishes may be at greater risk (Olden et al. 2007). Age at maturity is also linked to extinction probability—for example, in freshwater fishes (Parent and Schriml 1995), terrestrial mammals (Purvis et al. 2000b), and marine fishes (Denney et al. 2002)—almost certainly because of its negative association with maximum population growth rate (Cole 1954). Litter or clutch size (fecundity in fishes) has divergent associations with extinction probability in some groups—negative correlation in land mammals (Purvis et al. 2000b), positive association in birds (Jiguet et al. 2007)—or none at all in others,

such as marine fishes (Hutchings 2001). Unsurprisingly, narrow distributional range (e.g., Purvis et al. 2000b, Long et al. 2007) and low abundance (e.g., Purvis et al. 2000b, O'Grady et al. 2004) have also been associated with greater risk of extinction. We present a summary of these and additional life-history, ecological, and behavioral correlates in table 1.

Prominent among anthropogenic correlates of risk are those that affect habitat (Dulvy et al. 2003, Venter et al. 2006, Schipper et al. 2008), one generic (albeit indirect) metric of which is road density within a species' range (Chu et al. 2003). For some taxonomic groups, such as freshwater fishes, physical alterations to habitat may make it difficult to reliably distinguish the biological correlates of extinction risk from those associated with habitat degradation (Duncan and Lockwood 2001, Reynolds et al. 2005a, Olden et al. 2007). A second dominant correlate is exploitation pressure effected by unsustainable rates of fishing or hunting (Dulvy et al. 2003, Hutchings and Reynolds 2004, Schipper et al. 2008).

Notwithstanding the considerable strengths of the analyses undertaken to date, because most have been restricted to a single taxonomic class or subclass (table 1), it is unclear how broadly applicable the results might be across different taxonomic groups within a specific conservation or management region in which species status assessments are often undertaken. Generality may also be compromised by an inconsistency in analytical techniques, by inconsistent choices of potential extinction-risk correlates (and differing units of measurement), and by differences in the habitats or distributional scales of the species of interest (e.g., temperate, tropical, marine, freshwater, terrestrial, coral reef environments). There is also the question of how

Table 1. Life-history, ecological, and behavioral correlates of extinction risk in vertebrates.

Positive correlate of extinction risk	Taxonomic group	Sources
Large body size	Terrestrial mammals	Cardillo and Bromham 2001, Cardillo 2003, Cardillo et al. 2005, Davidson et al. 2009
	Marine mammals	Dulvy et al. 2003
	Freshwater fishes	Olden et al. 2007
	Marine fishes	Jennings et al. 1998, Denney et al. 2002, Dulvy et al. 2003, Reynolds et al. 2005b, Field et al. 2009
	Birds	Bennett and Owens 1997, Norris and Harper 2004
Small body size	Freshwater fishes	Reynolds et al. 2005a, Olden et al. 2007
Age at maturity	Terrestrial mammals	Purvis et al. 2000b
	Freshwater fishes	Parent and Schriml 1995
	Marine fishes	Denney et al. 2002, Myers and Worm 2005, Reynolds et al. 2005b
Small litter or clutch size	Terrestrial mammals	Purvis et al. 2000b
	Birds	Bennett and Owens 1997, Krüger and Radford 2008
Small distributional range	Terrestrial mammals	Purvis et al. 2000b
	Freshwater fishes	Reynolds et al. 2005a
	Birds	Long et al. 2007, Manne et al. 1999
Low latitudinal midpoint	Freshwater fishes	Reynolds et al. 2005a
Low density or population size	Terrestrial mammals	Purvis et al. 2000b, Davidson et al. 2009
	Birds	O'Grady et al. 2004
Trophic position	Terrestrial mammals	Purvis et al. 2000b
Low natal dispersal/migration	Birds	Jiguet et al. 2007

different scales of examination (e.g., spatial, taxonomic) might affect the influence of extinction-risk correlates. Differences in ecology or life history also predispose species to respond differently to various threats. With birds, for example, habitat specialists appear to be particularly vulnerable to habitat loss (Owens and Bennett 2000).

In light of the limitations to achieving generality associated with performing multiple analyses on different traits across scales, we adopted a common analytical and statistical approach in order to examine a common suite of potential extinction-risk correlates across a wide range of vertebrates, including terrestrial and marine mammals, freshwater and marine fishes, and birds. We constructed predictive models of risk status that accounted for the influence of life history (e.g., age at maturity, clutch or brood size, body size), distribution (e.g., latitude, aquatic depth), and anthropogenic disturbance (e.g., road density, fishing; table 2). Spatially, our analysis was restricted to species in Canadian aquatic and terrestrial environments. The primary reason for focusing on Canadian ecosystems lies in the breadth and wealth of available data on more than 600 species at risk. The information is published by COSEWIC (Committee on the Status of Endangered Wildlife in Canada; www.cosewic.gc.ca), the national independent body legally responsible, under the Species at Risk Act, for advising the federal minister of the environment on species that warrant inclusion on the national list of species at risk. Our work builds on that undertaken by Venter and colleagues (2006), who charac-

terized threats across taxonomic groups within Canada by directly comparing at-risk and not-at-risk species.

Data sources and analysis

The vertebrate species included in our study were those assessed by COSEWIC as being at risk as of March 2008. For the purposes of our analysis, we combined species assessed as extinct, extirpated, endangered, threatened, or of special concern into a single “at-risk” category. To form a comparison data set of sufficient but similar size, we used lists of species in Canada (e.g., www.wildspecies.ca) to randomly select 50 “not-at-risk” species for each of the five vertebrate groups. Taxonomic affiliation is unlikely to have a significant effect on our results, given that the species assessed as being at risk and not at risk were not generally taxonomically biased (see tables S1–S5 in the supplementary online materials at dx.doi.org/10.1525/bio.2011.61.7.8). We used online databases (table 2) to collate data on candidate extinction-risk correlates for the not-at-risk species; for the at-risk species, we consulted COSEWIC status reports and recovery strategies (www.sararegistry.gc.ca) and supplemented these data using online databases. Where multiple values were present, we recorded the mean. Where values for both male and female members of a species were available, we recorded the values for the female members. Data on amphibians and reptiles were excluded because of either a paucity of life-history information or an insufficient number of species with which to compare the at-risk and

Table 2. Ranks assigned to potential correlates of extinction risk.

Potential correlates	Terrestrial mammals	Marine mammals	Freshwater fishes	Marine fishes	Birds	Description
Age at maturity	1	2	1	1	2	Age at maturity (in years)
Life span	c	c	c	c	d	Maximum reported age (in years)
Size at maturity	c	c	c	c	2	Length or height at maturity (in millimeters)
Maximum size	2	1	2	2	d	Maximum length or height (in millimeters)
Gestation time	2	2				Gestation average (in months)
Number of eggs or litter size	2	d	d	d	2	Number of eggs or offspring
Size of eggs or offspring	c	c	d	d	c	Egg diameter (fish, in millimeters), egg length × height (birds, in millimeters squared), or offspring mass (mammals, in grams)
Altricial or precocial					2	Altricial or precocial young
Latitude midpoint			3	3		Midpoint between the maximum and minimum latitudes (in degrees)
Depth midpoint			d	2		Midpoint between the maximum and minimum depths (in meters)
Road density	1		d		1	Median road length in range (in meters per square kilometer)
Fishing intensity				3		Commercial fishing intensity (from FishBase: 1, no interest; 2, subsistence or minor commercial; 3, commercial; 4, highly commercial)
Data sources	AnAge database (www.genomics.senescence.info/species), Animal Diversity Web (www.animaldiversity.ummz.umich.edu)	AnAge database (www.genomics.senescence.info/species), Animal Diversity Web (www.animaldiversity.ummz.umich.edu)	FishBase (www.fishbase.org), Scott and Crossman 1973	FishBase (www.fishbase.org), Scott and Crossman 1973	Birds of North America Online (www.bna.birds.cornell.edu/bna), Patuxent Bird Identification InfoCenter (www.mbr-pwrc.usgs.gov/infocenter), Natureserve (www.natureserve.org)	

Note: Data-deficient variables (d) and collinear variables (c; variance inflation factor ≥ 5 or $r \geq .7$) are shown here but were not included in candidate model sets. Numbers indicate relative importance ranking for each variable, according to summed Akaike weights of models containing that variable (a rank of 1 identifies the variables of greatest importance; values within a relative importance of 0.1 of the next most important variable are denoted with the same rank). In the case of the collinear variables, we chose those that had the most support in the literature and were the easiest to collect reliably.

not-at-risk groups. Frequency distributions of the candidate extinction-risk correlates, which we illustrate as beanplots for visual-comparative purposes (figure 1; Kampstra 2008), show all the data, including those deemed to be either excessively collinear (see below) or of insufficient sample size or data quality to include in the modeling process (table 2). We did not include range size in our models, given that it is frequently used in classifying species as at risk (figure S1), and we were concerned that our results might then be confounded by the listing criteria.

As a proxy for human disturbance of terrestrial habitat, we calculated road density as the median length of

roads, in meters per square kilometer, from road network coverage maps available from GeoGratis (Government of Canada; www.geogratis.ca) within the species' Canadian terrestrial ranges. For the marine fishes, we used a discrete metric of human impact reported in FishBase (www.fishbase.org), called *commercial fishing intensity*, which we grouped into four classes: (1) no interest, (2) subsistence fishery or minor commercial interest, (3) commercial interest, and (4) high commercial interest. The lack of range maps for 55% of the freshwater fish species in our data set (Scott and Crossman 1973) prevented us from including nearby road density as a potential correlate for

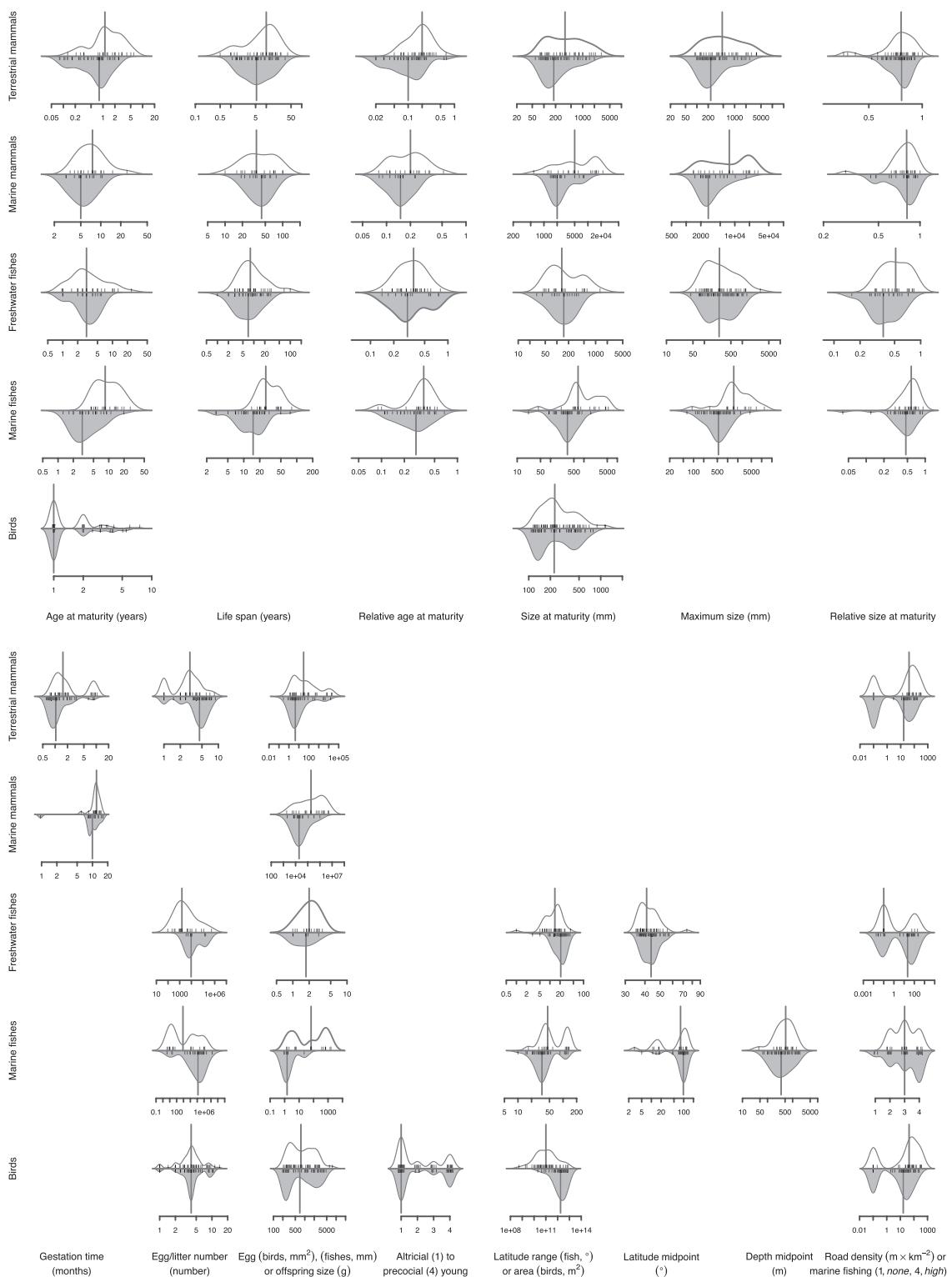


Figure 1. Beanplots of potential correlates of extinction risk for five groups of vertebrate species in Canada. The short vertical lines indicate species for which data are available. The estimated density of the distribution of values is shown for at-risk (white) and not-at-risk (gray) species in the form of curved polygons (beans). The median of each distribution is shown with a long vertical black line. Note the log-distributed horizontal axes. Missing plots were either data deficient (depth midpoint for freshwater fishes, range area for terrestrial and marine mammals, life span and maximum size for birds) or not applicable (all others). Relative age at maturity is the age at maturity divided by life span. Relative size at maturity is the size at maturity divided by maximum size. Abbreviations: g, grams; m, meters; mm, millimeters; $m \times km^{-2}$, meters per square kilometer; °, degrees.

freshwater fishes in the predictive modeling portion of our analysis. The few existing data on metrics of past harvest intensities for Canadian marine mammals prevented us from including a metric of human-associated extinction risk for this taxonomic group.

We constructed predictive models of species risk status (at risk versus not at risk) using generalized linear models with a binomial family and a logit link in a multimodel framework. The resulting logistic regression can be expressed as

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 x_{1,i} + \dots + \beta_k x_{k,i}$$

where p_i is the estimated probability of being at risk for a given species i , β_0 is an intercept, and β_1 through β_k are the coefficients of independent variables $x_{1,i}$ through $x_{k,i}$. The k covariates used to fit the models were selected on the basis of their potential importance as extinction-risk predictors, as it was determined by previous research (see table 1), and the ease with which they could be measured reliably. We excluded collinear variables (for which the variance inflation factor was greater than five; Menard 1995) and variables that were highly correlated ($r \geq .7$) with one another (table 2). Finally, we used variables for which values were available for at least 50% of both the at-risk and the not-at-risk species. We fit all candidate models with the k covariates as main effects and generated averaged predictive models by ranking the models by their Akaike information criterion with a correction for small sample sizes (AIC_c; Sugiura 1978, Burnham and Anderson 2002) and averaging the coefficients on the basis of their Akaike weights (see the supplementary online materials for full details of the multimodel analysis).

Model evaluation

We evaluated the predictive performance of the models by carrying out 10-fold cross-validations (Stone 1974, Kohavi 1995). For each taxonomic group, we divided the data into 10 subsets, retaining 1 subset for validation while fitting each candidate model to the remainder of the data. We repeated the process for each subset before repeating the entire 10-fold cross-validation procedure 1000 times to obtain an average misclassification rate (MR) for each candidate model. Ten-fold cross-validation is commonly used in this sort of investigation because lower-fold (two- or five-fold) validations often introduce greater variation because of the limited size of the training data and because higher-fold validations (e.g., the leave-one-out method) can introduce increased bias (Kohavi 1995). Receiver operating characteristic curves provide a measure of model performance at different prediction cutoffs. The area under such curves (AUC) represents the probability that a given species will be categorized correctly. We report the MR and AUC values both for comparison with the AIC_c ranking and as a method for comparing model performance across taxonomic groups.

Given that the International Union for Conservation of Nature (IUCN) Red List criteria are used as a starting point for discussion of a species' status in COSEWIC assessments, that the Red List criteria indirectly use generation time as a method to scale time-based life-history parameters, and that generation time is related to age at maturity (Cole 1954), we conducted two additional analyses to ensure that any correlates identified here were not purely a consequence of their having been used to assess species status. First, we tested whether generation time was positively related to scaled population decline for at-risk species within one taxonomic group (marine fishes), the taxonomic group for which magnitude of population decline is most often used as a basis for assessing status (figure S1). Second, given that the IUCN Red List criteria are not used to assess whether species are of special concern, we tested the sensitivity of our results by comparing special-concern species with not-at-risk species (i.e., excluding extinct, extirpated, endangered, and threatened species).

Analysis of relative life-history traits

As an additional exploratory analysis, we also tested for differences in relative age at maturity (age at maturity divided by life span) and relative size at maturity (size at maturity divided by maximum size) between the at-risk and the not-at-risk species. We reasoned that the differences in somatic and reproductive investment indicated by these variables could affect risk status. For example, those species that mature late relative to their life spans might not readily be able to depend on a lengthy reproductive period of life to offset greater mortality. We did not include these relative measures at our predictive modeling stage for two reasons. First, we lacked strong prior empirical support for doing so (these measures had not been examined previously). Second, their inclusion would have generated an excessive number of candidate models, given our data set sizes, and would have reduced our capacity to make valid predictive inferences (Burnham and Anderson 2002). We excluded birds from this part of the analysis because of uncertain and imprecise determinations of maximum natural life spans (which can exceed 50 years in pelagic seabirds; Holmes and Austad 1995) and maximum body sizes for all but a small number of species. We fit logistic regressions modeling risk status as a function of relative life-history traits within each taxonomic group.

Results of the analysis

The candidate extinction-risk correlates in our analyses were generally—although not always—characterized by unimodal distributions (figure 1). In addition to allowing for a visual comparison of median and modal values between the at-risk and not-at-risk species, the beanplots illustrate the breadth of data that were typically available for each of the 14 potential correlates within each vertebrate group. After removing the species with incomplete data for all investigated variables in our models, our sample sizes ranged from 14 to 40 for the not-at-risk species and from 16 to 29 for the at-risk species (table S6).

Based on the values of the Akaike weights (w_i) and Δ_i ($AIC_{c(i)} - AIC_{c(\min)}$, where $AIC_{c(i)}$ is the AIC_c value for model i and $AIC_{c(\min)}$ is the smallest AIC_c value in the set of models), our analyses revealed support for more than one model within each of the five taxonomic groups (largest $w_i = 0.44$, between two and four models with $\Delta_i < 2$; table 3). As a consequence, we incorporated all of the candidate models (including those with $\Delta_i \geq 2$) into the averaged model for each group of species (figures 2 and 3; table S7). The resultant models for terrestrial mammals and marine fishes performed well ($AUC = 0.80\text{--}0.93$, $MR = 0.22\text{--}0.34$, for models with $\Delta_i < 2$; table 3), whereas the predictive models were less accurate for the marine mammals (best two models, $AUC = 0.67\text{--}0.74$, $MR = 0.34\text{--}0.35$), freshwater fishes ($AUC = 0.55\text{--}0.77$,

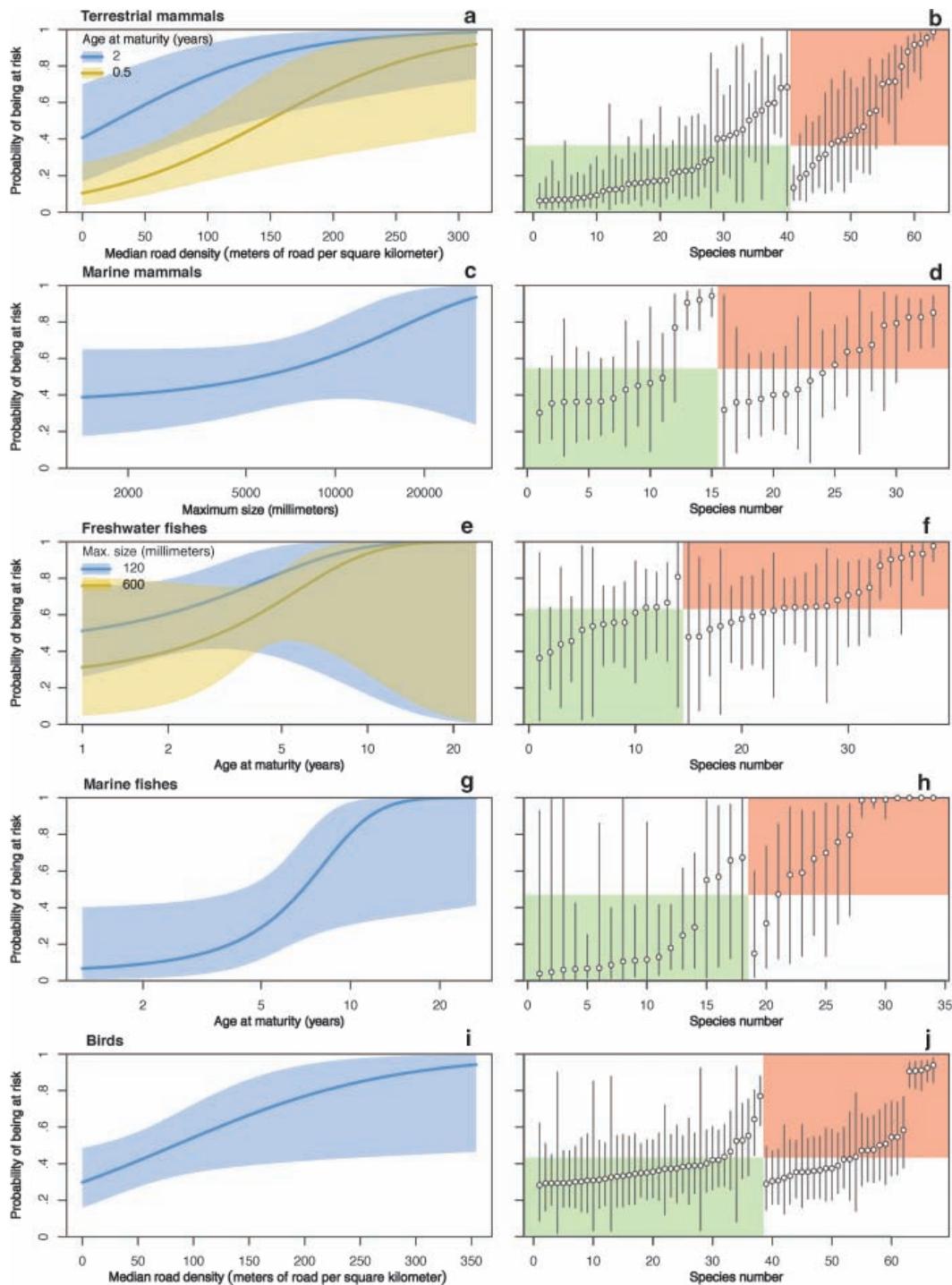
$MR = 0.36\text{--}0.42$), and birds (best two models, $AUC = 0.66\text{--}0.70$, $MR = 0.39\text{--}0.43$; table 3). The misclassification rate based on the averaged predictive models was lowest for the marine fishes ($MR = 0.18$) and highest for the marine mammals ($MR = 0.39$; figure 2).

Among all of the variables examined, age at maturity was the most consistently important (and positive) correlate of risk status, ranking among the most important variables for the terrestrial mammals, freshwater fishes, and marine fishes (figures 2a, 2e, 2g, and 3; table 2; table S7). Although there was some evidence that risk declined with maximum size in the freshwater fishes, there was less evidence of a link between maximum size and status for the marine fishes, for which the data suggested a weakly positive association

Table 3. Summary of the logistic regression models having the greatest support for each of the five vertebrate groups under study.

Model	$I(\theta)$	K	AIC_c	Δ_i	w_i	MR	AUC
Terrestrial mammals							
am, rd	-31.39	3	69.18	0.00	0.32	0.32	0.80
am, gt, rd	-30.94	4	70.58	1.40	0.16	0.34	0.82
ms, am, gt, rd	-29.93	5	70.91	1.73	0.13	0.33	0.83
ms, am, rd	-31.22	4	71.13	1.95	0.12	0.33	0.80
Marine mammals							
ms	-19.29	2	42.98	0.00	0.44	0.35	0.67
ms, gt	-19.03	3	44.88	1.91	0.17	0.34	0.74
Freshwater fishes							
ms, am, lm	-20.51	4	50.23	0.00	0.41	0.37	0.77
ms, am	-22.52	3	51.75	1.51	0.19	0.36	0.66
am	-23.89	2	52.11	1.88	0.16	0.42	0.55
Marine fishes							
ms, am	-12.54	3	31.87	0.00	0.15	0.28	0.90
am	-13.78	2	31.95	0.08	0.14	0.30	0.90
ms, am, dm	-11.31	4	32.00	0.13	0.14	0.23	0.93
am, dm	-12.74	3	32.27	0.40	0.12	0.22	0.91
Birds							
rd	-41.85	2	87.88	0.00	0.22	0.40	0.66
en, rd	-41.37	3	89.12	1.23	0.12	0.40	0.70
ap, rd	-41.44	3	89.26	1.37	0.11	0.41	0.68
am, rd	-41.53	3	89.44	1.56	0.10	0.43	0.66
sm, rd	-41.59	3	89.57	1.68	0.09	0.39	0.67

am, age at maturity; ap, altricial or precocial young; dm, depth midpoint; en, egg number; fi, fishing pressure; gt, gestation time; lm, latitude midpoint; lr, latitude range; ls, litter size; ms, maximum size; ra, range area; rd, road density; sm, size at maturity. AIC_c , Akaike's information criterion with a correction for finite sample sizes; AUC, area under the receiver operating characteristic curves; K, the number of parameters; $I(\theta)$ the value of the maximized log-likelihood function; MR, 10-fold cross-validated misclassification rates averaged over 1000 runs; w_i , Akaike weight; Δ_i , $AIC_{c(i)} - AIC_{c(\min)}$, where $AIC_{c(i)}$ is the AIC_c value for model i and $AIC_{c(\min)}$ is the smallest AIC_c value in the set of models. The models are ordered by decreasing w_i and only those with $\Delta_i < 2$ are shown.



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Figure 2. Panels (a), (c), (e), (g), and (i) show the predicted risk status for five groups of vertebrate species calculated from averaged logistic models. Estimates (dark blue and yellow lines) and 95% unconditional confidence intervals (shaded areas) are shown. The variable with the greatest relative importance (according to the sum of the Akaike weights of the models containing each variable) is shown across its range of values on the horizontal axis (note the log-distributed horizontal axes). Other variables were set to their median values. Where two variables were of similar relative importance (within .1 on a scale of 0 to 1), the second most important variable is shown with separate lines set at approximately the first and third quartile values. Panels (b), (d), (f), (h), and (j) show the classification of the five data sets based on the averaged model. Estimates (circles) and unconditional confidence intervals (lines) are shown. The bottom left green panel indicates correctly classified not-at-risk species. The top right red panel indicates correctly classified at-risk species. Species are ordered by increasing predicted probability of being classified as at risk.

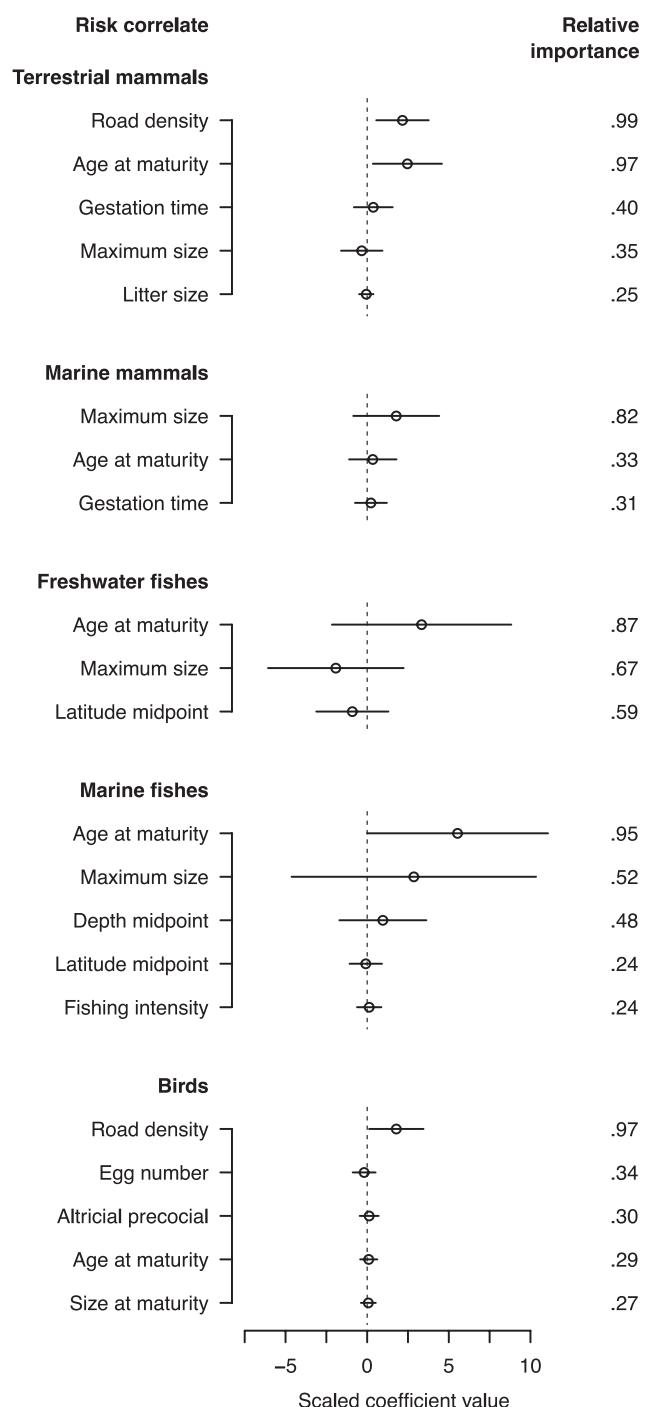


Figure 3. Scaled model parameter estimates (circles) with 95% unconditional confidence intervals (lines) from averaged predictive logistic models of risk status for the five taxonomic vertebrate groups under study. The parameters are ordered within each vertebrate group by their relative importance (indicated on the right) to the averaged model on a scale of 0 to 1. In this figure, the data were scaled within each vertebrate group by subtracting the mean and dividing by two standard deviations (Gelman 2008) to allow for comparison among parameters and across groups.

(relative importance = .83 and .52, respectively). For the marine mammals, maximum body size was the most important (and positive) predictor of risk status (figures 2c and 3), although there was relatively low confidence in this assessment and the performance of the averaged model was relatively poor (figure 2d).

Among the distribution-related variables, there was weak evidence that the marine fishes inhabiting deeper waters and the freshwater fishes in lower latitudes were more likely to be at risk (figure 3). In the taxonomic groups for which metrics of anthropogenic impact were readily available (terrestrial mammals, marine fishes, and birds), road density was associated with increased risk of extinction in the terrestrial mammals and birds (figures 2a and 3).

Our data did not support the hypothesis that generation time was directly related to the reported magnitude of population decline (figure S2). Our main conclusions for the terrestrial mammals, freshwater fishes, and marine fishes were not altered when we compared only the species of special concern with the not-at-risk species (figures S3, S4, and S5). For the marine mammals, maximum size (the most important correlate within the taxonomic group) changed from being a weakly positive correlate to being a weakly negative correlate, but the revised confidence interval was wide and included the original estimate (figure S5). The positive road density coefficient for birds became weaker (figure S5).

Our additional exploratory analyses testing for the influence of two relative life-history traits identified patterns consistent with the results obtained from the averaged predictive models. Controlling for differences in life span, (relative) age at maturity was greater for the at-risk species than for the not-at-risk species in the terrestrial mammals (coefficient estimate = 4.66, 95% confidence interval = 0.27–9.05; figures 4a and 5). Controlling for differences in maximum size, (relative) size at maturity was greater for the at-risk species than for the not-at-risk species in the freshwater fishes (coefficient estimate = 5.50, 95% confidence interval = 0.71–10.28) and the difference was nearly significant for the marine fishes (figures 4b and 5).

Correlates of risk status

The present study is both exploratory and confirmatory in nature. It is exploratory in the sense that one objective was to determine which correlates of risk status would emerge from a large data set on a previously unexamined group of species within a spatially delimited region across a wide range of vertebrates (figure 1). Furthermore, we explored possible links between risk status and two relative life-history metrics that—to our knowledge—had not been previously examined in this context. It is confirmatory in the sense that we tested a subset of previously hypothesized correlates of risk and confirmed many as being of primary importance for predicting risk status of vertebrates in Canada (figures 2 and 3).

The relative importance of the extinction-risk correlates of species at risk in Canada differed among our five groups of terrestrial and aquatic vertebrates. Road density and age at maturity were the most important (and positively

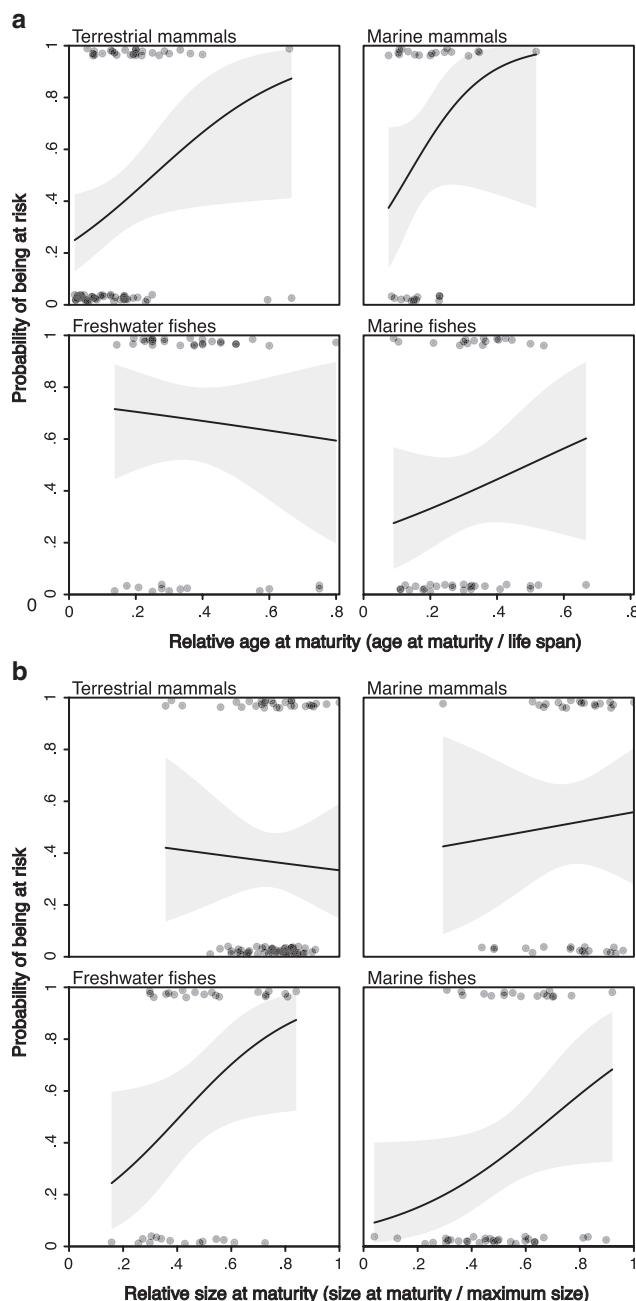


Figure 4. Estimates and uncertainty for the effect of relative age (a) and size (b) at maturity on the probability of a species being classified as at risk. The black lines represent fitted logistic regressions, the shaded areas represent 95% confidence intervals, and the dots represent the individual species represented by the data to which the models were fit (a small amount of vertical jittering was added for clarity).

associated) determinants of at-risk status in the terrestrial mammals. For the freshwater and marine fishes, age at maturity (positive correlate) was of primary importance and maximum size (negative correlate) was of secondary importance. For the marine mammals, larger individuals may bear a greater risk than smaller individuals. In the birds,

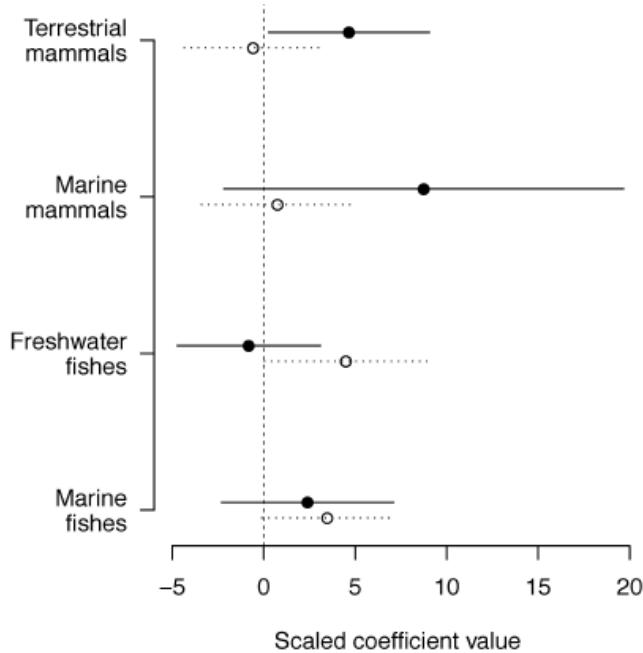


Figure 5. Scaled coefficients of relative age at maturity (solid symbols) and relative size at maturity (open symbols) with 95% confidence intervals from logistic regressions predicting probability of a species being at risk. The data were scaled within each vertebrate group by subtracting the mean and dividing by two standard deviations to allow for comparison among parameters and across groups.

the primary determinant of at-risk status was greater road density. Although some of these correlates are consistent with previous work (table 1), others are not, and we discuss these similarities and dissimilarities in greater detail below.

We found strong evidence for high road density and late age at maturity as predictors of terrestrial mammal risk status. Road density, our metric of terrestrial anthropogenic impact, has frequently been correlated with risk in terrestrial mammals (Cardillo et al. 2004, 2005, 2008, Benítez-López et al. 2010). The finding that late age at maturity correlates with risk concurs with Purvis and colleagues' (2000b) work. However, in contrast to some studies (Purvis et al. 2000b, Cardillo et al. 2005, Davidson et al. 2009), we found less evidence in Canadian terrestrial mammals that risk status increases with body size. Although the beanplot for maximum size (figure 1) suggests that at-risk terrestrial mammals tend to be larger and maximum size was correlated with age at maturity ($r = .64$), there was less evidence for its importance when it was compared with other correlates in the multimodel analysis (figure 3). Although we used maximum length in our analysis rather than mass (to ensure that we had consistent units across taxa in our analyses), it is unlikely that our results can be explained by a different unit of measure, given the high correlation ($r = .96$) that exists between the logarithm of maximum length and the logarithm of maximum mass in our data set. Substituting body mass for body length in our multimodel-averaged analysis did not affect our conclusions.

For the marine mammals, there was little evidence that any of the variables in our data set were associated with risk status, other than the limited effect that we documented for body size. The lack of dominant extinction-risk correlates at the taxonomic scale considered here would, however, justify efforts to explore the existence of such correlates at a finer taxonomic scale. Analyses that distinguish pinnipeds and cetaceans from one another, for example, may well yield further insights into the identification of factors affecting risk. We would also note that the low classification success in our model for marine mammals might be attributable to a comparative lack of information on past and present anthropogenic factors that might affect risk status (e.g., historically intensive exploitation rates, current levels of incidental catch).

Our analyses provided some evidence that older age at maturity and smaller maximum body size are positive correlates of extinction risk in freshwater fishes. In contrast to the (weak) positive correlation of larger maximum body size with risk status for marine fishes, the opposite effect may be evident for freshwater fishes because of higher levels of habitat loss and degradation (Olden et al. 2007). Although we detected some evidence that smaller maximum body size was associated with greater risk, this pattern was only evident after removing incomplete rows of data (such as those used in the multimodel analysis; figure S6) and not with the complete data set (figure 1). Although the distribution of the data (figure 1; figure S6) does not rule out Olden and colleagues' (2007) hypothesis that both large and small freshwater fishes are at greatest risk, the form of the predictive logistic regression model did not allow us to investigate the hypothesis explicitly (figure 2e). There was little evidence of the effect of latitude midpoint that Reynolds and colleagues (2005a) had documented for freshwater fishes in Europe. This may be attributable to the relatively narrow latitudinal range occupied by Canadian freshwater fishes at risk, most of which are located adjacent to the US border in the west and in southwestern Ontario and to southeastern Quebec in the east (Hutchings and Festa-Bianchet 2009).

The capability of our models to predict risk status in marine fishes was better than that in any other taxonomic group. Age at maturity was the most important correlate of risk, a finding concordant with the results of previous studies (Denney et al. 2002, Reynolds et al. 2005b). Commercial fishing interest was of minimal influence as a risk correlate, an observation contrary to expectations that fishing mortality affects extinction probability in marine fishes (e.g., Hutchings 2001, Hutchings and Reynolds 2004). This discrepancy can almost certainly be attributed to the imperfect degree to which present or past fishing mortality is reflected by the four-point measure of current fishing interest analyzed here. A more comprehensive analysis of the extinction risks posed by fishing would include an examination of the degree to which magnitude of population decline and current population status relative to some conservation-based target were correlated with temporal changes in levels of fishing mortality.

Our data suggested a pronounced association between small range area and bird species endangerment consistent with the findings of previous studies (Manne et al. 1999; Long et al. 2007). However, range area may be confounded with the explicit determinants of the COSEWIC decisionmaking process (figure S1), and so it was not included as a predictor in our formal analysis. Accordingly, we found that road density was the most influential (positive) correlate of bird risk status. Elevated road densities seem to have negative effects on the local population densities of many bird species (Fahrig and Rytwinski 2009, Benítez-López et al. 2010). For many birds that are already at low numbers—in particular, ecological specialists adapted to narrow habitat niches (Owens and Bennett 2000)—the progression to endangerment is therefore more likely as road density and its associated habitat disruption increase. Collectively, the precedence of road density in predicting bird species' endangerment over other intrinsic life-history parameters (large body size, Norris and Harper 2004; small clutch size, Krüger and Radford 2008) suggests that in Canada, habitat loss (i.e., a reduction in niche availability) is the most important process driving bird endangerment.

Implications for species status assessment

Our study of the biological and anthropogenic correlates of extinction risk in Canadian vertebrates represents a logical taxonomic and analytical extension of previous research. To achieve an arguably greater degree of spatial and taxonomic generality, we undertook analyses across five large and diverse groups of vertebrates that were consistent in the variables considered, the models applied, and the spatial scale examined. Although one might argue that with such an approach, the importance of some extinction-risk correlates for certain species might not be detected, our intent was to attain a level of generality across taxonomic groups able to inform national (e.g., COSEWIC) and international (e.g., IUCN) efforts to apply consistent methodologies and criteria to assess extinction risk across widely diverse taxa. In this regard, age at maturity was the most important correlate of at-risk status among the 14 life-history, distribution, and anthropogenic variables examined here, a finding supportive of the scaling of the IUCN's various decline-related criteria and thresholds to species and population generation times.

One unavoidable caveat associated with our work is that the correlates of risk that we have identified are based on past rather than future conditions. This means that changes to extinction risks posed by climate change (which has been identified as a threat to an increasing number of species in Canada, such as Peary caribou, *Rangifer tarandus pearyi*; polar bear, *Ursus maritimus*; and beach pinweed, *Lechea maritima*; www.sararegistry.gc.ca) will not have been accounted for in our analyses. Although some of the correlates of risk evaluated here may be relatively robust to climate change (e.g., road density), others (such as geographical range) may be more susceptible to climate-related influences, particularly in a country such as Canada, in which significant changes in terrestrial biodiversity attributable to global warming are anticipated (Lawler et al. 2009).

From an assessment perspective, we suggest that there may be considerable promise in the logistic modeling approach adopted here. First, functions such as those depicted in figure 2 serve to illustrate qualitatively, for different groups of species, how different variables are related to the probability of those species being at risk. Second, one could use the values associated with the risk-status functions (defined by the forward or backward S-shaped part of the curves in figure 2) to define trait thresholds in species status assessments. For example, for marine fishes inhabiting Canadian waters, using the data accumulated to date, one could apply a threshold age at maturity of 5 to 10 years to distinguish species that may be at heightened extinction risk. The extent to which one would adhere strictly to such thresholds would depend on the slope of the curve (the shallower the slope, the broader the range of values encompassing the threshold) and on the width of the 95% unconditional confidence intervals associated with the model (the greater the width, the greater the uncertainty in the threshold).

In summary, we draw three primary conclusions from our analyses. From a methodological perspective, there is utility in applying consistent analytical techniques (and consistent units of measurement) to studies of extinction-risk correlates across multiple taxonomic groups within a single spatially discrete region. Second, the correlates identified here may prove helpful in undertaking assessments for data-limited species within the context of a precautionary approach to assessing extinction risk. That is, all else being equal, species of concern for which a correlate of risk suggests heightened extinction probability might be afforded a higher protection status than those for which a correlate does not. Third, we suggest that logistic regression offers an instructive means of identifying correlates of extinction risk and of applying them in a practicable, readily understandable, and empirically defensible manner in species status assessments. Broadscale examinations such as the one we have undertaken here may also serve to enhance empirical support for the broadly articulated and widely applied extinction-risk criteria often used by international and national assessment organizations.

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